

A REVIEW OF THE GENUS *PHILETOR*
(CHIROPTERA : VESPERTILIONIDAE)

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A REVIEW OF THE GENUS *PHILETOR* (CHIROPTERA: VESPERTILIONIDAE)

By J. E. HILL

SYNOPSIS

The genus *Philetor* is reviewed and its geographical distribution extended from New Guinea to Malaya by the inclusion of *Eptesicus verecundus* Chasen, 1940. Particular attention is given to features considered of value in determining the affinities of the genus within the Vespertilioninae and its relationships are examined in detail.

INTRODUCTION

THE vespertilionid genus *Philetor* with type species *P. rohui* was described by Thomas (1902) from a series of ten specimens obtained in the Albert Edward Mountains, Papua, New Guinea. Since that time, additional specimens of *P. rohui* from New Guinea have been received by the British Museum (Natural History) and, with the original series, these form the basis of this brief review. At the same time, an examination has been made of the holotype of *Eptesicus verecundus*, described by Chasen in 1940 from Malaya and apparently so far known only from this and one other specimen. The holotype proves referable not to *Eptesicus* but to *Philetor*, Chasen having failed to note the salient features of the external genitalia and skull. The major features of *Philetor* as thus understood have been studied with a view to establishing the relationships of this small but interesting genus.

PHILETOR Thomas

Philetor Thomas, 1902: 220. Type species *Philetor rohui* Thomas.

A study of the genera *Pipistrellus*, *Nyctalus*, *Eptesicus*, *Tylonycteris* and *Mimetillus* indicates that apart from its curiously specialized external genitalia (which are approached in some respects by *Tylonycteris* and *Mimetillus*) there are no other exclusive diagnostic characters which serve to isolate *Philetor* as sharply as was thought by Thomas or by Miller (1907: 213). However, it may be distinguished readily by a number of features in combination. The wings are narrow, with the fifth digit much reduced, its total length equal approximately to the combined length of the metacarpal and one-half of the length of the first phalange of the fourth digit. The braincase is high and rounded, the supraorbital region inflated with prominent supraorbital tubercles. The inner upper incisor (i^2) is bifid and is long and narrow in contrast to the outer upper incisor (i^3), which is small and conical. There is a prominent secondary posterior upper canine cusp and the small anterior upper premolar (pm^2) is lacking. The sole upper premolar (pm^4) and the second lower premolar (pm_4) are very much shortened so that their length at the cingulum is equal to approximately one-half of their width and at the alveolus is equal approximately to one-third of their width. The third upper molar (m^3) is not reduced and has three well-defined commissures.

Philetor rohui Thomas

The head is short and broad, with a wide, flattened muzzle, the narial openings sublateral, widely separated and not projecting. The anterior part of the muzzle is sparsely clothed with hair, with a distinct fringe of hairs on the upper lip. The ears are short, triangular in outline and rounded at the tip. There is a small lobe at the base of the anterior margin of the ear, above which the anterior margin is strongly convex near its base but is otherwise straight or nearly so, the posterior margin of the ear being slightly convex in its upper and lower parts, these separated by a shallow concavity. There is a small antitragal lobe, the posterior margin of the ear terminating behind and slightly below the angle of the mouth. There are a few sparse hairs on the anterior part of both the internal and external faces of the ear. The tragus is short, thick and fleshy, its anterior margin straight for its basal half but otherwise slightly convex, the upper part of the tragus slightly prolonged anteriorly. The upper margin of the tragus is slightly convex and its posterior margin slightly so or straight, with a small triangular lobe near the base. This lobe is absent in the holotype of *verecundus* but apparently has been destroyed during the extraction of the skull from the specimen in alcohol. The wing is narrow, with the fifth digit much reduced, its total length exceeding the length of the metacarpal of the fourth digit only by one-half of the length of the first phalange of the fourth digit. The metacarpal of the fifth digit is by far the shortest of the metacarpals and the combined lengths of the two terminal phalanges of the fifth digit are equal only to the length of the first phalange of the third digit. The thumb is short and stout. There is a distinct post-calcarial lobe supported by a robust calcar which extends along approximately one-half of the length of the posterior margin of the interfemoral membrane.

The genus is remarkable in the extraordinary complexity of the structure of the external genitalia. The penis (Text-fig. 1a-b) is long, with a stout shaft and large, prominent glans. It is densely pilose only at its base. Distally, the dorsal surface of the shaft (Text-fig. 1a) bears a cushion-like pad, on occasion divided to some extent by a longitudinal median depression. For much of its area this pad is moderately clothed with short, stiff bristles. The ventral surface of the shaft (Text-fig. 1b) is prolonged distally by a projecting preputial flap or fold, the slender stem of the glans penis emerging between its lateral lips which each bear a tuft of moderate, rather stiff hairs. According to Thomas (1902 : 221) the penis of *Philetor* lacks a prepuce: however, it seems evident that the flap or fold projecting from the lower part of the penial shaft is the lower or ventral lip of the prepuce, its upper or dorsal lip forming the anterior margin of the curious cushion-like pad which embellishes the distal part of the dorsal surface of the shaft. The glans penis is a swollen, approximately triangular structure pierced on its dorsal surface near the tip by the urethral opening. It is supported by a slender, upwardly curved stem which emerges from the tip of the shaft a little below its centre. Ventrally, the stem extends beneath the swollen glans penis almost to the tip and it is bordered by lateral fissures in the body of the glans: the underside of the stem has a median

longitudinal groove extending almost to the point of emergence from the prepuce (Text-fig. 1*b*). The os penis or baculum (Text-fig. 1*c-e*) is strongly curved dorso-ventrally (Text-fig. 1*d*) and has a wide, deep flanged base, slender shaft and an expanded tip. Viewed dorsally (Text-fig. 1*c*) the base of the os penis forms a

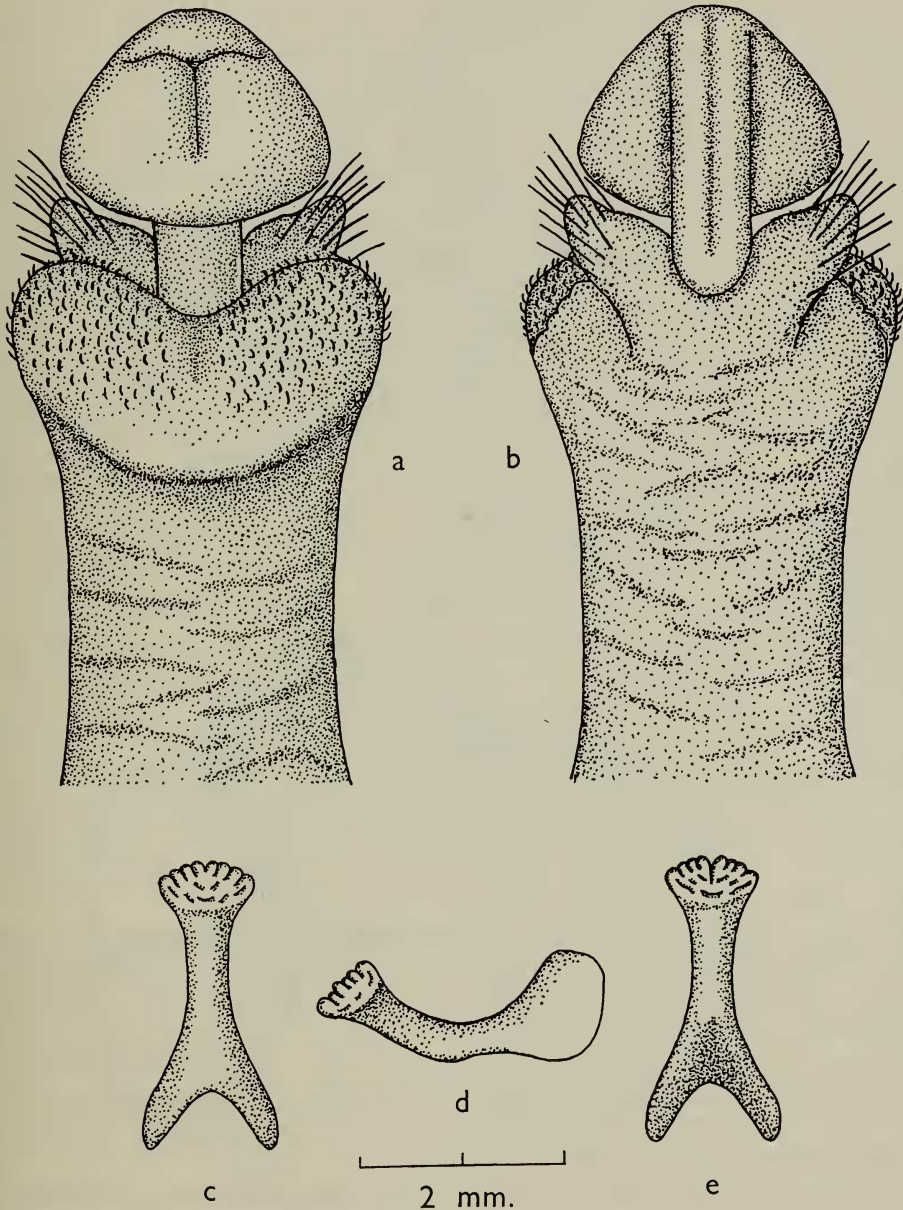


FIG. 1. *Philetor rohui rohui*. a, dorsal aspect of penis; b, ventral aspect of penis; c, dorsal aspect of os penis; d, lateral aspect of os penis; e, ventral aspect of os penis.

solid, bifid structure: ventrally (Text-fig. 1e) the base is hollowed, the medial groove thus formed extending to the base of the stem. As suggested by Thomas, the paired basal flanges evidently support the cushion-like pad on the dorsal surface of the penial shaft and the enlarged tip of the os penis supports the glans.

The external genitalia of the female (Text-fig. 2a-b) are similarly complex. The vulval opening is separated from the anus by paired, swollen perineal cushions or pads (Text-fig. 2a) which are divided by a median longitudinal groove and which have their surfaces sparsely covered with short hairs. Anterior to the vulval opening and normally partially concealing it there is a wide, subtriangular pad, partially divided longitudinally by a shallow median trough, its base anteriorly situated and with its apical part directed posteriorly and immediately above the vulval opening. This fleshy pad clearly corresponds to the prepuce of the male and a well-developed glans clitoridis emerges from the fleshy fold forming its apical part (Text-fig. 2a). It is separated from the perineal pads by deep lateral fissures. There is a slightly swollen area forming a low cushion immediately posterior to the anus. The vulval opening is transverse, but also extends anteriorly as a narrow longitudinal slit (Text-fig. 2b) between fleshy lips, each with a small projecting spur posteriorly where they form the anterior rim of the transverse part of the vulval opening. No doubt this longitudinal slit led Thomas (1902: 221) to his statement that the vulva was longitudinal instead of transverse: in fact the actual opening is transverse but is prolonged longitudinally. Posteriorly, the rim of the vulval opening is formed by the anterior walls of the perineal pads, which extend inwards in shelf-like fashion to form its posterior margin. Normally, the apical part of the subtriangular anterior pad fits into the shallowly V-shaped margin formed by the anterior part of the two perineal pads, thus concealing the vulval opening. The glans clitoridis is normally concealed within the apical folds of this pad, its tip only being exposed. Thomas (1902: 221) suggested that it appears probable that the slender projecting tip of the glans penis alone enters the vulva and the arrangement of cushion-like pads on the dorsal surface of the penis and on the perineum of the female supports this conclusion. The bristly pad on the dorsal surface of the penial shaft evidently engages with the perineal pads of the female during copulation while the tip of the glans clitoridis engages in the groove beneath the stem supporting the glans penis.

All of the available specimens of *P. rohui* are preserved in alcohol. From these it appears that the dorsal surface of the body is uniformly dark brown, as is the head and nape: the ventral surface is similar in colour to the back but is slightly paler. As suggested by Thomas (1902: 221) from the original series, which was even then in a bad state of preservation, the fur is short and close. It does not extend appreciably on to the flight membranes except for a sprinkling of fine hairs on the ventral surface of the wing from the body to a line joining the elbow and knee and for a few sparse hairs at the root of the tail.

The skull is short and wide, with short, wide, rounded braincase, its frontal part elevated. There is a slight occipital helmet with sharp lambdoidal ridges in older specimens. The sagittal crest is weak, dividing anteriorly into weak supraorbital

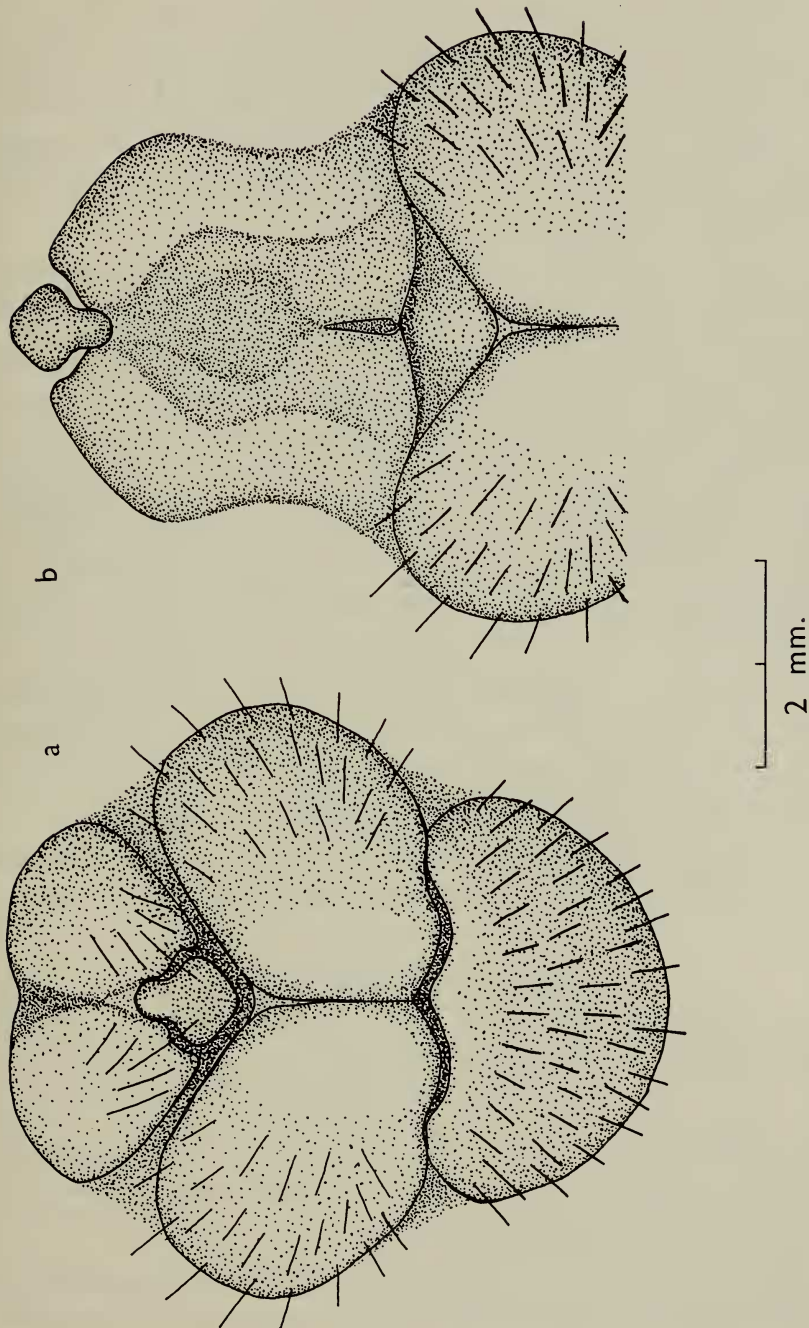


FIG. 2. *Philetor rohui rohui*. *a*, female external genitalia; *b*, vulval opening exposed.

ridges which terminate in prominent supraorbital tubercles. The interorbital region is broad and the rostrum wide and rather high, the anteorbital foramen enclosed by a comparatively wide bar of bone. The zygomata are slender, in older specimens with a small inferior projection anteriorly, external to m^3 . They are slightly widened posteriorly. The narial emargination is deep, extending posteriorly to a line joining the supraorbital tubercles and almost halfway to the interorbital constriction. The anterior palatal emargination is deep and is wide posteriorly, slightly chordate in outline, in older specimens with a median anterior palatal spine. The palate is short, wide and domed, with a large, blunt, ligulate post-palatal spine. The meso-pterygoid fossa is wide and there are moderate basial pits: the bullae are high and are slightly inflated.

The inner upper incisor (i^2) is elongate, narrow, and bicuspid, the posterior or outer cusp a little smaller and lower than the anterior or inner cusp. The outer upper incisor (i^3) is small and conical, its height only slightly exceeding the cingulum height of i^2 , with a well-developed cingulum in contact or nearly so with the inner tooth. It is separated from the canine by a moderate diastema. The upper canine has a prominent posterior secondary cusp extending for one-third to one-half of the height of the tooth. The upper premolar (pm^4) is short, its length at the cingulum equal to approximately one-half of its width and it is tightly compressed between the canine and the first upper molar (m^1). The upper molars exhibit no especial peculiarities: m^3 is not reduced and has a prominent metacone and three well-defined commissures. The lower incisors are tricuspid and are not imbricated. They are situated in the line of the toothrow and are not turned at all transversely to it. The outer lower incisor (i_3) is very slightly wider than i_1 or i_2 . The lower canine has small anterior and posterior cingulum cusps. The anterior lower premolar (pm_2) is equal in height to the second lower premolar (pm_4) and is comparatively unreduced, its length at the cingulum equal approximately to its width. The second lower premolar (pm_4) is much reduced, its length at the cingulum rather less than one-half of its width and with its posterior face hollowed where it engages with the anterior face of pm^4 . Its crown area is equal to or barely exceeds the crown area of pm_2 . The lower molars have no unusual features.

Philetor rohui rohui Thomas

Philetor rohui Thomas, 1902: 220. Albert Edward Mountains, Papua, New Guinea, 6,000 ft.

Narial emargination not abruptly widened just above the roots of i^{2-2} . Minimum, maximum and (in parentheses) mean measurements (in millimetres) of fourteen specimens, except where stated: length of forearm (twenty specimens) 31.3-35.5 (33.4); greatest length of skull 13.4-14.8 (14.3); condylobasal length (thirteen specimens) 12.9-14.0 (13.6); least width of interorbital constriction 4.3-4.8 (4.6); zygomatic width (four specimens) 10.3-10.7 (10.5); width of braincase 7.3-8.2 (7.8); c- m^3 (front of canine to crown of m^3) 4.4-4.9 (4.7).

This subspecies is known so far only from New Guinea. It is recorded from specimens in the Archbold Collections of the American Museum of Natural History from

Oomsis, Morobe District and Kassam, Highlands District, in the Territory of New Guinea by Brass (1964 : 180, 204) who also (1956 : 136) records it from Biniguni Camp, Gwariu River, Papua, again from the results of the Archbold Expeditions. Tate (1942 : 265) records a specimen in the Archbold Collections from the Idenburg River, West Irian. Laurie (1952 : 313) recorded a series of specimens from Enaena, on the north-eastern slopes of Mount Simpson, eastern Papua, in the collection of the British Museum (Natural History). This collection also contains specimens from Dinawa, Owen Stanley Range, Papua and from Madeu, inland from Port Moresby, Papua. These are the specimens mentioned by Tate (1942 : 265).

***Philetor rohui verecundus* (Chasen)**

Eptesicus verecundus Chasen, 1940 : 53. Mount Kladang, Perak, Federation of Malaya, 2,646 ft.

Narial emargination abruptly widened just above the roots of i^{2-2} . Chasen described *Eptesicus verecundus* from two specimens originally in the collection of the Raffles (now National) Museum, Singapore. That designated as the holotype is preserved in alcohol, with the skull extracted and was collected in November, 1916 by Dr. R. Hanitsch. Originally Raffles Museum No. 199, it was transferred to the British Museum (Natural History) in 1947 and is now B.M. 47.1437. The second example, also in alcohol with the skull extracted, came from an unspecified locality in Perak and remains in the National Museum, Singapore (Gibson-Hill, 1949 : 171). So far as I am aware, no further specimens have been obtained.

The original description compared *Eptesicus verecundus* with *E. pachyotis* (Dobson) and *E. demissus* Thomas, Chasen noting that it was smaller than either of these species. He remarked also that compared with *pachyotis* the body of *verecundus* is larger in relation to the wings, "as in *demissus*". He had available for comparison specimens of *pachyotis* from the Khasia Hills, Assam, "very kindly sent to Singapore from the Indian Museum, Calcutta as the types of *pachyotis* some years ago . . ." and gives measurements of the length of forearm and lower leg with foot in these specimens. He states that the skulls had not been extracted, and his brief description of *verecundus* omits any mention of the structure of the external genitalia or of cranial features beyond noting that the inner incisor is much the larger and is tricuspid and that the upper canines have a small posterior secondary cusp. The description is otherwise concerned with external features such as the point of insertion of the wing membrane on the leg, and with the ears and tragus : he draws attention to the presence of a distinct post-calcarial lobe. Tate (1942 : 279) says "*Verecundus* obviously has peculiarities not seen elsewhere in *Eptesicus*" apparently solely on the basis of the published description.

An examination of the holotype of *Eptesicus verecundus* shows that in fact it is not an *Eptesicus* but is referable to *Philetor*, agreeing in almost every respect with *P. rohui* and differing only in a few minor and relatively insignificant points. The wing is reduced to almost exactly the same extent, with the fifth digit extending as far as a point slightly more than half-way along the first phalange of the fourth digit. The external genitalia of the female holotype are exactly as described for *P. rohui*. Cranially, there is a high degree of agreement but the braincase is a little

more inflated than in *P. rohui* and the narial emargination is more abruptly widened just above the roots of i^{2-3} , with a broadly V-shaped apex. Although the supra-orbital region has been damaged on both sides of the skull, the left side retains a prominent supraorbital tubercle: the corresponding tubercle on the right side of the skull has been lost. The inner upper incisor (i^2) is elongate and narrow, bicuspid, with a faint trace of a third posterior cusp which doubtless led Chasen to describe it as tricuspid. Measurements (in millimetres) of the holotype of *verecundus*: length of forearm 34.0; greatest length of skull —; condylobasal length 14.5; least width of interorbital constriction 4.7; zygomatic width —; width of braincase 7.9; c-m³ (front of canine to crown of m³) 4.7. The very close measure of agreement in structure and size between *verecundus* and *rohui* indicates that specific separation is unwarranted and for the present I consider them to be but subspecifically related.

The allocation of *verecundus* to *Philetor* clearly raises some question as to the status of *Eptesicus pachyotis* and *E. demissus*. The precise status of *E. pachyotis* seems uncertain (Tate, 1942: 277) and unfortunately the collections of the British Museum (Natural History) contain no specimens referable to it. The descriptions by Dobson (1871: 211, 1876: 104, figs., 1878: 206) are insufficient to enable any firm conclusions to be drawn, and the question must remain in abeyance until the holotype (Dobson, 1878: 206) can be re-examined. It is presumably in the Indian Museum, Calcutta, whence Dobson described it. The collection of the British Museum (Natural History), however, does include the holotype of *E. demissus*. Externally, there is some similarity between this species and *verecundus* but *demissus* is considerably larger and the wings are not reduced, the fifth digit not conspicuously shortened but with its metacarpal nearly as long as the metacarpal of the fourth digit and with its tip reaching almost to the end of the first phalange of the fourth digit. The external genitalia of the female holotype lack the specialisations of *verecundus*. Cranially, the two are markedly dissimilar. The skull of the holotype of *demissus* is damaged but sufficient remains to demonstrate the presence of an occipital "helmet" and of a prominent sagittal crest. As Tate (1942: 277) pointed out, the roof of the narial canal and of the anterior part of the mesopterygoid fossa is raised: in *verecundus* these lie deep in the skull. The inner upper incisor (i^2) of *demissus* is massive and wide, quite unlike the elongate, narrow i^2 of *verecundus*. The outer upper incisor (i^3) is wide, its width exceeding its length, and has a large central cusp flanked by small lateral cusps. There is a low secondary posterior canine cusp but pm^4 is not shortened: i_{1-3} are considerably imbricated and pm_4 is not reduced, its length at the cingulum nearly equal to its width and its crown area exceeding that of pm_2 . There seems no doubt that *demissus* has no close relationship to *verecundus* and thus to *Philetor* but instead apparently constitutes a distinct group within *Eptesicus*.

RELATIONSHIPS

Thomas (1902: 220) considered *Philetor* allied to *Vespertilio* (= presumably to *Eptesicus* as understood by Miller (1907: 207)), *Tylonycteris* and *Hesperoptenus*, also drawing attention to its resemblances to *Pterygistes* (= *Nyctalus*). Miller (1907: 214)

remarked that *Philetor* appeared related to *Tylonycteris* although lacking the flattening of the skull found in that genus. Subsequently, Tate (1942 : 266) thought that *Philetor* and *Tylonycteris* might be independently derived from near the *joffrei* group of *Pipistrellus*, and noted (pp. 252, 253, 265) the resemblances between the members of this group and *Philetor*. Evidently the relationships of *Philetor* are likely to be found within this complex of genera and their associated species: the absence of the small pm^2 in *Philetor* no doubt has influenced earlier authors in suggesting relationship to those genera in which this evanescent tooth is absent rather than to those in which it is present.

There appears to be no close relationship to *Hesperoptenus*, which has wings of normal proportions with the fifth digit unreduced in length. Although some modification of the penis has occurred in this genus, it is of a different nature to the specialisation of the penis in *Philetor*, as Thomas (1902 : 221) pointed out. In *Hesperoptenus* the prepuce is much developed and although the os penis is similarly divided at the base to that of *Philetor*, it is a much longer structure, straight and not upwardly curved and not expanded at its tip. Cranially, the braincase of *Hesperoptenus* is not elevated anteriorly and there are no supraorbital tubercles. The inner upper incisor (i^2) is a massive, unicuspid tooth, not elongate and narrow as in *Philetor* and i^3 in some species is displaced inwards to such an extent that it is situated behind the inner tooth. There is no secondary posterior canine cusp and pm^4 are not shortened antero-posteriorly as in *Philetor*, with pm_2 much reduced.

Externally, there is a close resemblance between *Philetor* and *Eptesicus* but in that genus the wing is not reduced as it is in *Philetor*. The frontal part of the braincase is not elevated and there is little or no inflation of the supraorbital region. Prominent supraorbital tubercles are not developed in *Eptesicus*. Although bicuspid, i^2 is not elongate and narrow as in *Philetor* and i^3 is not especially reduced although smaller than the inner tooth. There is no secondary posterior canine cusp and pm^4 are not shortened. The lower incisors are usually imbricated and pm_2 is reduced as in *Hesperoptenus*.

There is stronger evidence for a degree of relationship with *Tylonycteris*. As Tate (1942 : 266) has remarked, if the flattening of the skull in this genus be disregarded, then cranially and dentally it has a very close resemblance to *Philetor*. Externally, it differs from *Philetor* in the presence of pads on the thumbs and feet and the wing is not reduced but the penis has some similarity to that of *Philetor* and consists of a strong shaft with a large, expanded terminal pad like that of *Philetor*, similarly embellished with short, bristly hairs. On the dorsal surface of the shaft the pad is divided by a median longitudinal fissure to form swollen lateral cushions but ventrally it is less swollen although extending completely across the width of the shaft. There is no preputial fold such as is found in *Philetor* and the small glans penis emerges directly from a terminal perforation. The female external genitalia display none of the peculiarities of *Philetor*. There are no perineal pads although the vulval area is slightly swollen, and the vulval opening is wholly transverse without any median longitudinal extension. Cranially, there is some expansion of the supraorbital region in *Tylonycteris*, coupled with a varying degree of develop-

ment of supraorbital tubercles, minimal in *T. pachypus* and its allies, maximal in *T. robustula* and *T. malayana*. There is on occasion a small, rather poorly-defined inferior zygomatic projection external to m^3 and the post-palatal spine is ligulate as in *Philetor*. The inner upper incisor (i^2) is elongate and narrow as in *Philetor*. It is similarly bicuspid, the posterior cusp as high or almost as high as the anterior cusp. The outer upper incisor (i^3) differs from that of *Philetor* and has a large central cusp equal in height or nearly equal in height to the posterior cusp of i^2 , flanked by two smaller lateral cusps. It is slightly hollowed posteriorly. In *Philetor* this tooth is peg-like and conical: a faint trace of lateral cusps can be found only in the holotype of *verecundus*. The upper canine of *Tylonycteris* has a strong secondary posterior cusp and pm^4 is slightly shortened much as in *Philetor*, its length at the cingulum equal approximately to one-half of its width. The lower incisors (i_{1-3}) are slightly imbricated and pm^2 is but slightly reduced and is almost equal in height to pm^4 , which is shortened in the same way as it is in *Philetor*, its length at the cingulum equal to one-half or to a little less than one-half of its width and its crown area equal to or only slightly exceeding the crown area of pm^2 .

Great reduction of the wing is found in the Ethiopian genus *Mimetillus* which resembles *Tylonycteris* in the presence of pads on the thumbs and feet and to which it has been considered (Allen, 1939: 194) to be related. In *Mimetillus* the reduction of the wing is not confined only to shortening of the fifth digit as in *Philetor* but extends also to shortening of the third digit, a feature unremarked in any other bat. The penis of *Mimetillus* does not resemble that of *Tylonycteris* or of *Philetor* at all closely. It is long and is wide at the base, tapering to a narrow tip. The shaft has no terminal pad such as occurs in these genera, its conical distal half instead being only slightly expanded and covered with short, bristly hairs. There is a small terminal opening through which protrudes the glans penis. The female external genitalia display some similarity to those of *Philetor*. The vulval opening is separated from the anus by paired, small poorly-developed perineal pads and there is a prominent posteriorly directed fold anterior to the opening which covers it and is slightly triangular in outline, a fissure at the apex indicating the glans clitoridis. The vulval opening is wholly transverse and has no median longitudinal extension as in *Philetor*. The skull of *Mimetillus* is flattened as is the skull of *Tylonycteris* and the supraorbital region is much widened by the great degree of inflation of the maxillaries above the anteorbital foramina: as Tate (1942: 266, footnote) has pointed out, these swellings are not strictly homologous with the supraorbital tubercles of *Tylonycteris* (and *Philetor*) but instead are "swellings of the area anterior to that part of the orbit which encloses the anteorbital foramen, but posterior to the foramen". It is the upper part of the bar enclosing the foramen and the part of the maxilla immediately adjacent which is swollen. The zygomata are massive, in contrast to the slender zygomata of *Philetor* and *Tylonycteris*. The inner upper incisor (i^2) is less markedly elongated than in *Philetor* or *Tylonycteris* but is bicuspid as it is in those genera. The outer upper incisor (i^3) is almost exactly like the corresponding tooth in *Tylonycteris*. There is no secondary posterior canine cusp but pm^4 is reduced to about the same extent as it is in *Philetor* and *Tylonycteris*,

its length at the cingulum equal approximately to one-half of its width. The lower incisors are imbricated. There is a marked difference between *Mimetillus*, *Philetor* and *Tylonycteris* in the proportions of the lower premolars: in *Mimetillus* pm_2 is very much reduced, almost peg-like, its height not exceeding one-half of the height of pm_4 and its crown area approximately one-quarter of the crown area of that tooth, which is not especially shortened, its length at the cingulum rather more than one-half of its width. Despite some similarities to *Philetor* and to *Tylonycteris*, a number of features of *Mimetillus* indicate that it has no very close relation to either of these genera, and Tate (1942: 266) has remarked that certain of its characteristics suggest that it may be of independent origin.

In the original description Thomas (1902: 220) noted that *Philetor* resembled *Nyctalus* in its general appearance and in its much shortened fifth finger. It must be remembered, however, that at the time that Thomas wrote, the genus *Nyctalus* was held to include the species *joffrei*, *stenopectus* and *brachypterus* subsequently removed by Tate (1942: 252) to form the *joffrei* group of *Pipistrellus*. There is no immediate connection between *Philetor* and *Nyctalus* as thus restricted. As understood by Tate, *Nyctalus* has a high, convex frontal region and high rostrum as in *Philetor* but the rostrum is less widened and supraorbital tubercles are lacking. There is no inferior zygomatic projection and the post-palatal process is spine-like. The inner upper incisor (i^2) is massive, its length equal approximately to its width, and its posterior cusp is obsolete. The outer upper incisor (i^3) is wider than long and is deeply concave posteriorly, with a small secondary posterior cusp. There is no secondary posterior canine cusp and pm^2 is present, pm^4 being only slightly shortened. The lower incisors are imbricated and pm_2 is much reduced, its crown area one-half or less than one-half of the crown area of pm_4 .

The nearest relatives of *Philetor* appear to be found in the *joffrei* group of *Pipistrellus* (more correctly the *brachypterus* group), created by Tate (1942: 251) to include the three species *joffrei*, *stenopectus* and *brachypterus*, all formerly included within *Nyctalus*, together with a fourth, *anthonyi*, which he described in that paper (p. 252). Ellerman and Morrison-Scott (1951: 159), however, retain *joffrei*: in *Nyctalus* but (p. 173) leave *anthonyi* in *Pipistrellus*. Of these four species, only *joffrei* and *stenopectus* are available to me. The members of the *joffrei* group have the wing reduced to a greater or lesser extent by shortening of the fifth digit. The rostrum in these species is short and wide, with incipient or moderately developed supraorbital tubercles and on occasion there is an inferior descending zygomatic process external to m^3 . The outer upper incisor (i^3) is small and a secondary posterior canine cusp is present: pm^2 is minute, pm_2 unreduced and pm^4 shortened antero-posteriorly. There is considerable justification for the removal of this group of species from *Nyctalus* since apart from the reduced wing and the presence of a minute pm^2 these features are anomalous in that genus as otherwise understood. In fact, the *joffrei* group of species displays a number of the features characteristic of *Philetor*. Tate (1942: 252) notes that the group approaches the Oriental members of the *savii* group of *Pipistrellus* in which pm^2 is minute and the palate shortened but which have not developed supraorbital tubercles.

So far as I am able to determine from the material available to me and from the literature *Pipistrellus joffrei* and *P. anthonyi* appear to be the most greatly modified members of the group. The collection of the British Museum (Natural History) contains the male holotype of *P. joffrei* B.M. 88.12.1.37, from the Kachin Hills, Burma, and also three female examples, B.M. 16.3.26.2, 83, 84, from 50 miles west of Kindat, Chindwin, Burma. The ear and tragus closely resemble those of *Philetor* and the fifth digit is correspondingly reduced, its metacarpal conspicuously shorter than the metacarpal of the fourth digit and its tip reaching a point approximately half-way along the first phalange of the fourth digit. The external genitalia (Text-fig. 3), however, differ from those of *Philetor* although in some respects those of the male conform closely to the same pattern. The penis (Text-fig. 3a-b) is shorter than that of *Philetor* and the dorsal surface of the shaft bears a similar but less developed bristly pad in its distal part. This pad is less swollen and less extensive than in *Philetor*. The preputial fold is well developed and originates a little below this rudimentary pad, from which it is clearly demarcated. It is sparsely scattered with short hairs and has a shallow median longitudinal fissure in its dorsal surface and a relatively large terminal opening. Through this protrudes the small glans penis, which is perforated near its tip by the urethral opening. So far as can be discovered, an os penis, if present, must be very small and rudimentary. The female external genitalia (Text-fig. 3c) are not specialized as in *Philetor*. There are no perineal pads as in that genus, the vulval area being only slightly swollen, and the vulval opening is wholly transverse with no median longitudinal extension. The lips of the vulva protrude slightly and the glans clitoridis is represented by a small protuberance immediately anterior to the vulval opening.

The skull of *Pipistrellus joffrei* is very like that of *Philetor* in its general appearance, but the braincase is more elevated posteriorly and a little less so anteriorly. The rostrum is rather less elevated and usually the supraorbital tubercles are not as much developed. There is a small inferior descending zygomatic process external to m^3 . The palate is relatively a little narrower than in *Philetor* and has a similarly ligulate post-palatal spine. The inner upper incisor (i^2) is elongate as in *Philetor* but is relatively very slightly wider. It is bicuspid as in that genus, the posterior cusp nearly as high as the anterior cusp. The outer upper incisor (i^3) is wide, less reduced than in *Philetor*, and is much hollowed posteriorly. It has a large central cusp flanked by smaller lateral cusps, the postero-external cusp obsolescent, the antero-internal cusp with a small subsidiary cusp below it. There is a well-developed secondary posterior canine cusp. The anterior upper premolar (pm^2) is very small and is situated in the angle or recess formed by the base of the posterior canine cusp, the postero-internal part of the canine cingulum and the anterior face of pm^4 , which is slightly shortened antero-posteriorly, its length at the cingulum a little more than one-half of its width. The third upper molar is unreduced, with a well-developed metacone and three commissures. The lower incisors (i_{1-3}) are not imbricated and pm_2 is not reduced, its height nearly equal to that of pm_4 and its crown area equal approximately to the crown area of that tooth, which is slightly shortened antero-posteriorly, its length at the cingulum slightly exceeding one-half

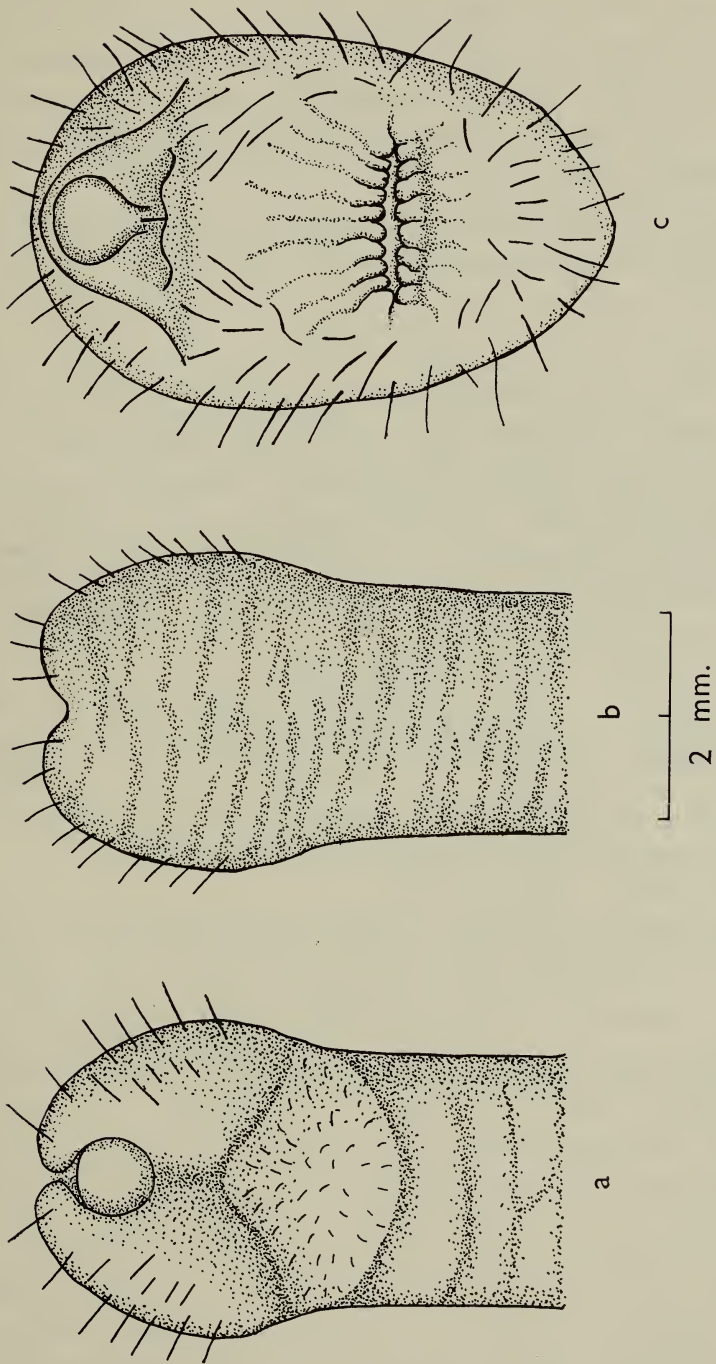


FIG. 3. *Pipistrellus joffrei*. a, dorsal aspect of penis; b, ventral aspect of penis; c, female external genitalia.

of its width. There seems little doubt from the description by Tate (1942 : 252) that *Pipistrellus anthonyi* is very closely related to *P. joffrei*, differing from this species only in colour and in minor cranial details. It appears to be known only from the male holotype, a dry skin with damaged skull, and no details of the external genitalia are available. The description and measurements suggest that it may approach even more closely to *Philetor* than does *Pipistrellus joffrei* in the widening of the rostrum, the degree of development of the supraorbital tubercles and the extent of the shortening of pm_1 .

The remaining species allocated to the *joffrei* group seem much less closely related to *Philetor* than are *Pipistrellus joffrei* or *P. anthonyi*. The ears and tragus of *P. stenopterus* are similar to those of *P. joffrei* but the wing is less reduced with the fifth digit less shortened, its metacarpal nearly as long as the metacarpal of the fourth digit and its tip reaching almost to the distal end of the first phalange of the fourth digit. The penis, although about the same length as in *P. joffrei*, lacks any rudimentary pad on the dorsal surface of its shaft and there is no preputial fold. It consists instead of a simple shaft with a median longitudinal fissure along its dorsal surface extending to a terminal opening. The female external genitalia are similar to those of *P. joffrei*. The skull is much like that of *P. joffrei* but the supra-orbital tubercles are less developed. The anterior upper premolar (pm_2) is relatively larger than in *P. joffrei* and pm_2 is unreduced, its height equal to that of pm_4 , which it exceeds in both length and width. The crown area of pm_2 is twice that of pm_4 , which is more reduced than in *P. joffrei*. From the description by Tate (1942 : 253) based on an alleged "co-type", *Pipistrellus brachypterus* seems very near to *P. stenopterus*, and, if the specimen described by Dobson (1876 : 92, 1878 : 223) from the Berlin Museum is correctly identified as *brachypterus*, then possibly these are conspecific or even synonymous. Of particular significance is the remark by Dobson concerning the Berlin specimen that its first lower premolar (pm_2) is slightly longer than and in transverse diameter nearly double the second (pm_4) and is also nearly equal to the canine in vertical extent.

The Vespertilioninae comprise a complex of closely interrelated genera separated in some instances by comparatively slender or even rather arbitrary distinctions and the pattern of relationship within the subfamily is often obscured by parallelism or convergence. However, there is substantial evidence to indicate a relationship between *Philetor* and the *joffrei* group of *Pipistrellus* and also between *Philetor* and *Tylonycteris*, although *Philetor* seems sufficiently removed from both *Pipistrellus* and *Tylonycteris* to justify its retention as a distinct genus, presenting as it does a combination of features not met with elsewhere. In a suggested phylogeny of the pipistrelloid genera, Tate (1942 : 233, fig.) derived *Philetor*, *Tylonycteris* and *Mimetillus* from a point on the *Pipistrellus* stem. I would endorse the view expressed by this author elsewhere in the same paper (p. 266) that *Philetor* and *Tylonycteris* are derived from near the *Pipistrellus joffrei* group and have lost the small pm_2 independently. In a number of respects the two genera display further extensions of trends evidently inherent in this group: in *Philetor* the external genitalia have become very much modified and *Tylonycteris* has developed additional specializations of

the thumbs, feet and braincase. There seems little doubt that *Philetor* and *Tylonycteris* are closely related but the affinities of *Mimetillus* are less certain. Although in some features it approaches *Philetor* and *Tylonycteris*, in others it differs markedly from both genera and, if not an indication of independent origin, these characteristics suggest no more than a remote relationship. The exact status of the *joffrei* group is open to some doubt. As Tate (1942: 252) suggests, it may warrant subgeneric recognition within *Pipistrellus* but it has not been possible to examine all of the species allocated to it and until this can be done its status must remain uncertain. There is insufficient evidence to justify its transfer to *Philetor* and in any event, only *joffrei* and *anthonyi* among its included species show any near approach to that genus.

SUMMARY

The genus *Philetor* is considered to remain monotypic but two subspecies of *P. rohui* are now recognized, the nominate subspecies being so far known only from New Guinea. *Eptesicus verecundus* Chasen, 1940, from Malaya, is not an *Eptesicus* but is referable to *Philetor*. It is very similar to specimens from New Guinea and is allocated to *P. rohui* as the second subspecies. A review of the structural features of *Philetor* and of other genera and species to which relationship has been postulated hitherto indicates that its affinities are with the *joffrei* group of *Pipistrellus* and with the genus *Tylonycteris*.

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